The following papers were read:—

1. On the Development of the Hyobranchial Skeleton of the Midwife-Toad (*Alytes obstetricans*). By W. G. Ridewood, D.Sc., F.L.S., Lecturer on Biology at St. Mary's Hospital Medical School, London.

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(Plate II.)

The object of the present investigation was to ascertain how far the peculiarities of the hyobranchial development of *Pelodytes*, already detailed in the Proceedings of this Society (9), are to be considered normal for phaneroglossal Anura generally. The adult hyobranchial skeleton of *Pelodytes* is so aberrant in structure that it is natural to suspect that the mode of development of the parts may not conform very closely with that of a more generalized type of Anuran. Since the arciferous type of shoudler-girdle, the presence of free ribs, the frequent persistence of postcardinal veins, and the primitive nature of the carpus and tarsus show *Alytes* to be one of the most lowly organized of the Anurous Batrachians, and in consideration of the larger size of the tadpoles of this genus as compared with those of the otherwise equally suitable genus *Discoglossus*, *Alytes* was chosen to supply the test.

The material for the investigation was, as before, generously provided by Mr. G. A. Boulenger, F.R.S., of the Natural History Museum, London. Twenty-one specimens were dissected, and from these the eight here described and figured were so selected as to exhibit the most even gradations from the youngest stage to the adult condition. The stages are numbered 1–8 to distinguish the order in which they succeed one another; but the use of these figures does not imply correspondence with any stage bearing a similar number in the previous descriptions of the hyobranchial skeleton of *Xenopus*, *Pipa* (8), and *Pelodytes* (9). In order to facilitate comparison the figures are not drawn to the same scale, but as nearly as possible of the same absolute size. The approximate magnification is given in each case. Figures 1–7 exhibit the dorsal surface of the hyobranchial skeleton, but fig. 8, of the adult, is drawn from the ventral surface, so that the ventral splint-bone may be more clearly seen. The method of procedure was the same as in the two earlier investigations; and as the nomenclature of parts adopted in this paper is the same as that previously employed in the description of the hyobranchial apparatus of *Pelodytes*, a lengthy introduction is here unnecessary.

The adult skeleton of *Alytes* (Plate II. fig. 8) is not very remarkable. The hyoidean cornua (*h*) are thin and continuous, but rather more flattened than in the Common Frog. The posterior cornua or thyrohyals (*t*) are normal, and in the middle of the ventral surface of the body of the hyoid is a V-shaped

superficial bone (*v*) which is related to the hyoglossus muscle in the same way as the H-shaped splint-bone of *Pelodytes*. The antero-lateral or alary processes (*pal*) and the postero-lateral processes (*ppl*) are feebly developed, but they are hardly so reduced in size as to justify the statement by Stannius (10. p. 65, footnote): "bei Alytes ist, statt zweier Seitenfortsätze, jederseits eine breite Platte vorhanden."

Of the published figures of the hyoid skeleton of *Alytes*, that by Parker (7. pl. 24, fig. 4) is the most reliable. This author regards the splint-bone as an ectosteal basibranchial (p. 134), and describes (p. 133) the hyoidean cornua as having small hypohyal lobes (= proc. ant. 9. p. 589), lobes which I find to be altogether wanting in the Discoglossid genera *Alytes*, *Discoglossus*, and *Bombinator*. The much earlier figure of Henle's (5. pl. 2, fig. 24), reproduced by Hoffmann in the 'Klassen und Ordnungen des Thierreichs' (6. pl. 46, fig. 24), is not much inferior to that of Parker's; but the one given by Dugès (2. pl. 3, fig. 20) is decidedly poor. Only the proximal ends of the hyoidean cornua are shown, and the lateral parts of the basal plate are represented in the figure, and described in the text (2. p. 56), as ossified in the same manner as in *Bombinator*. Cope (1. pl. 76, fig. 3) endeavoured to compromise matters by combining the figures of Dugès and Parker, from which fact it is evident that he had never seen the hyoid of *Alytes*, or he would have rejected Dugès's figure entirely. The statement by Cope (1. p. 234) that "sometimes the third ceratobranchial is ossified, as in Alytes (pl. 76, fig. 2)," involves a confusion of *Alytes* with *Bombinator*, for the figure referred to is that of the latter genus. The statement would, however, in neither case be correct.

Stage 1. *Specimen measuring from snout to root of tail* 20 *mm. Length of tail* 40 *mm. Length of hind limb* 2 *mm.* (Plate II. fig. 1.)

The ceratohyals (*ch*) are broad and flat at their mesial ends, while their lateral extremities bear each a convex surface for articulation with the palatoquadrate cartilage and a terminal process for muscular attachment. They are not in contact with one another in the median line, but between them occur first an elliptical cartilage, the anterior copula (*ca*), then a space, then a fibrous mass, the "pars reuniens" (*pr*), and finally a posterior copula (*cp*) of larger size than the first. The postero-internal edges of the ceratohyals abut on the hypobranchial cartilages (*hb*). The anterior copula ("erste Copula" of Gaupp, 3. pp. 411 and 412, to whom the discovery of this cartilage is due[1]) is elliptical in shape, the long axis of the ellipse being disposed at

[1] Götte (4. pl. 18, fig. 332) gives a figure of the larval hyobranchial skeleton of *Bombinator* showing three axial structures which probably represent the first and second copulæ, with the pars reuniens between. The relations, however, are not clearly indicated, and no special description is given of these parts in the text, so that the credit of the discovery of an anterior copula in Anuran tadpoles must be accorded to Gaupp.

right angles to the length of the body. It is united by fibrous tissue with the ceratohyal of each side, and is separated from the pars reuniens by a space or foramen. This latter is closed by loose connective tissue, and must not be confounded with the hyoglossal foramen of the aglossal Toads, transmitting the hyoglossus muscle. The pars reuniens is a dense mass of whitish fibrous tissue, with a straight anterior edge, slightly convex lateral margins, and a notched posterior border. It is slightly broader than long, and serves to bind the ceratohyals together. The second mesial cartilage, the posterior copula, corresponding with what was called "basihyal" in *Pelodytes* (9. p. 583), is much larger than the first. It is pentagonal in shape and considerably longer than broad. The pointed anterior end can be traced on the ventral surface of the pars reuniens, reaching as far forward as the foramen above mentioned, so that the length of the cartilage is greater than appears in a dorsal view. The antero-lateral edges abut on the ceratohyals, the lateral edges on the hypobranchial plates, while the posterior and smallest edge forms the anterior boundary of the laryngeal sinus. This complete separation of the hypobranchial plates by the second copula, which, like the presence of the anterior copula, is, I believe, peculiar to the Discoglossidæ, was incidentally referred to in my previous contribution (9. p. 581). There is in *Alytes* no triangular space on either side of the posterior copula such as occurs in *Pelodytes* (9. pl. 35, figs. 1, 2, and 3, *s*), *Pelobates*, and a great number of other genera.

The hypobranchial plates (*hb*) are approximately triangular in shape, and the posterior extremity of each bounds the laryngeal sinus laterally. The anterior angle runs up to the point where the ceratohyal and posterior copula touch one another, while the lateral angle is attached to the base of the first ceratobranchial (*cb* 1). The four branchial bars or ceratobranchials are united with one another at their proximal ends and at their distal ends. The last (*cb* 4) is the shortest and the broadest. The distal part of the third ceratobranchial is somewhat expanded, and is continued beyond the commissural cartilage into a pointed process which is much larger than those into which the ceratobranchials 1 and 2 are produced. There is no corresponding process to the fourth ceratobranchial. Five to eight warty outgrowths of cartilage occur on the anterior and posterior edges of the bars, but, while those on the posterior border of the fourth ceratobranchial are almost obsolete, those on the anterior border of the first ceratobranchial are greatly prolonged, so as to form a sort of palisade. There is a tendency for these latter processes to fuse in an irregular manner to form an anterior protective wall, as in *Pelodytes* (9. p. 584). Only three pairs of spicula are present. Those which constitute the free, recurved proximal ends of the third ceratobranchials are long (*sp* 3), but those of the second ceratobranchial are short and stunted. There are no spicula at all to the first ceratobranchial, and those of the fourth are continued back, as usual, over that posterior part of the

hypobranchial cartilage which will ultimately develop into the thyrohyal.

There is not the same continuity of ceratobranchial and hypobranchial cartilage as is found in *Pelodytes*; such coalescence, in fact, only occurs in the case of the fourth ceratobranchial. The third ceratobranchial is attached to the postero-lateral edge of the hypobranchial cartilage by fibrous tissue, while opposite to the place where the second ceratobranchial should be attached is a small foramen, the proximal end of the bar being kept in position only by its connections with the first and third ceratobranchials. Ceratobranchial 1 is attached by fibrous tissue to the lateral angle of the hypobranchial plate at some distance outward from the posterior cusp of the ceratohyal [1], and does not during later development become fused with it. There is thus an interesting difference between the relations of the proximal end of ceratobranchial 1 in *Alytes* and *Pelodytes*, for while in the latter genus it is fused with the hypobranchial cartilage and bound by connective tissue to the proximal end of ceratobranchial 2 (**9.** p. 584), in *Alytes* it is united with the hypobranchial by connective tissue and is fused with the end of the second ceratobranchial. The difference is important as well as interesting, inasmuch as the basal portion of the first ceratobranchial of *Pelodytes* can be clearly seen to persist as the postero-lateral process of the adult hyoid, while in *Alytes* the whole of the first ceratobranchial becomes absorbed, and the process of the hypobranchial cartilage to which it was attached broadens out into a plate from the edge of which the postero-lateral process (*ppl*) subsequently grows out (see figs. 5–7).

Stage 2. *Specimen measuring* 21 *mm. from snout to root of tail. Length of tail* 41 *mm. Length of hind limb, extended,* 19 *mm. Fore limbs extruded and measuring* 8 *mm. when extended.* (Plate II. fig. 2.)

Although at this stage the tadpoles have four well-formed legs, and have shed their horny jaws, but slight changes have occurred in the hyobranchial skeleton. The ceratohyals are larger and slope a little more posteriorly than in the first stage. The front copula is still present, but is smaller in proportion to the adjacent parts. The width across the hyoid region is now equal to the width across the branchial, whereas in the first stage it was less. The first ceratobranchial exhibits a wrinkling at its distal end, the absorption of cartilage having already begun in this position; and the laryngeal sinus is larger than before.

[1] Herein probably lies the explanation of the view propounded by Gaupp in his paper on *Rana* (**3.** p. 403), that the part of the first branchial arch between the spiculum and the hypobranchial plate belongs to the latter cartilage rather than to the ceratobranchial. There is no indication of any separation of the cartilages in *Rana* tadpoles, but as this author had, judging by his remarks on page 411 of his treatise, already made an examination of the larval hyobranchial skeleton of *Alytes*, it is just possible that his determination was influenced by the division which in this genus occurs in the position in question. The division is no more present in *Pelodytes* than in *Rana*, whence my hesitation (**9.** p. 584, footnote 2) to accept Gaupp's theory.

Stage 3. *Specimen measuring* 19 *mm. from snout to root of tail. Length of tail* 29 *mm. Length of hind limb, extended,* 21 *mm. Length of fore limb, extended,* 10 *mm.* (Plate II. fig. 3.)

The ceratohyals are more massive than before, and have acquired a distinct backward slope. Examined from the ventral surface, the two ceratohyals are seen to meet in the median line and to be overlapped (ventrally) by the tapering anterior end of the larger copula, although in the two preceding stages they were separated from one another by a distance equal to one-half of the total width of the pars reuniens. The pars reuniens itself is less conspicuous than before. The anterior copula has disappeared, and the hyoglossal sinus (*hgs*) thus makes its first appearance.

The posterior copula is now thicker than the hypobranchial plates; the two are flush above, but the copula projects ventrally. The future thyrohyals are assuming shape and are thicker than the surrounding cartilage. In fact, the cartilage immediately external to the middle part of the rod is already so much resorbed as to present an incipient foramen (*tf*), the "thyroid foramen" of the previous communication (9. p. 586). The fenestration does not begin exactly at the region of attachment of the thyroid bodies, but more posteriorly; the absorption, however, continues in a forward direction and also externally (see figs. 3 and 4). Since both the developing thyrohyals and the copula are thicker than the surrounding cartilage, the former appear to be processes of the latter, for the line of junction is no longer to be seen on the ventral surface, and is barely visible above.

Considerable reduction has occurred in the branchial skeleton, and it is chiefly this which is responsible for the new aspect which the whole hyobranchial skeleton has assumed. The ceratobranchials are not only thinner, but shorter than before, judging by the diminution in the length of the branchial clefts, so that a shrinkage of cartilage must occur as well as absorption, a fact already pointed out in the case of *Pipa* (8. p. 105) and *Pelodytes* (9. p. 588). The distal end of the first ceratobranchial has separated from its commissural cartilage, but the second and third clefts still remain enclosed. The spicula have practically disappeared, and the warty outgrowths on the ceratobranchials are mostly absorbed.

Stage 4. *Specimen measuring* 18 *mm. from snout to cloaca. Tail reduced to* 3 *mm. Length of hind limb, extended,* 21 *mm. Length of fore limb, extended,* 10 *mm.* (Plate II. fig. 4.)

The hyoglossal sinus is wider than before, and the ceratohyals slope more backwardly and are much more slender, especially at their distal or posterior ends. Here the surfaces of articulation with the palatoquadrate cartilage are no longer distinguishable. The pars reuniens has entirely disappeared, and the two ceratohyals can, in a dorsal view, be seen to unite in the median line. In Stage 3 this was only visible ventrally. A central oval area is differentiating in the middle of the hyobranchial skeleton. Its outline, though faint and ill-defined in front, is sharply marked behind, and

is caused partly by the now indistinct lateral limits of the second copula, but mainly by the white fibrous tissue, from which the ventral splint-bone will later develop, showing through the thickness of the cartilage.

The absorption of cartilage in the hypobranchial plates has proceeded apace, and the thyroid foramina are now quite large crescentic spaces. One of the consequences of this absorption is that the lateral promontory of the hypobranchial plate to which the first ceratobranchial is attached now stands out boldly at right angles to the median plane. On the anterior edge of this process a new cartilage is developing. It is as yet distinct from the hypobranchial cartilage, but in Stage 7 it fuses on, and forms part at least of, the alary or antero-lateral process of the adult hyoid (see figs. 4–7). A pair of cartilages similarly placed are figured by Parker in the hyobranchial skeleton of a recently metamorphosed specimen of *Rana palustris* (7. pl. 5, fig. 9), but he speaks of them (p. 37) as "remains of the branchial pouches," a determination which their position shows to be untenable.

The absorption of hypobranchial cartilage by the enlargement of the thyroid foramina causes the ceratobranchials to be *drawn in*, so that the proximal ends of ceratobranchials 2 and 3, which in Stage 3 were in a line with the extremity of the thyrohyal and the proximal end of the first ceratobranchial, are now much closer to the middle line. This, of course, is partly to be accounted for by the growth in length of the thyrohyals. The general result is that a transverse line drawn through the posterior ends of the thyrohyals now passes behind the branchial skeleton, whereas in the preceding stage the line passed through it. The fourth ceratobranchial has almost disappeared, only its distal end, fused with the external edge of the posterior extremity of the thyrohyal, remaining.

Stage 5. *Specimen measuring* 17 *mm. from snout to cloaca. Stump of tail* 1 *mm. Length of hind limb, extended*, 23 *mm. Length of fore limb, extended*, 10 *mm.* (Plate II. fig. 5.)

The ceratohyals are slightly longer than before and considerably thinner. The distal or posterior end is curved, and the part which forms the lateral boundary of the hyoglossal sinus is quite slender. The hyoglossal sinus itself is both broader and deeper. In Stage 4 the ceratohyals were in contact in the middle line, but they are now considerably separated, and the extent of their divarication is marked by two slight notches at the bottom of the hyoglossal sinus. There is evidently an absorption of cartilage taking place here, which causes the posterior copula to extend into the sinus. The side margins of the posterior copula are still to be seen, but since the fibrous predecessor of the ventral splint-bone underlies them, it is only possible to obtain convincing proof of the fact after removal of this superficial tissue. The lines run down to the antero-internal border of the thyroid foramen, and reach the hyoglossal sinus in front at the notches already indicated.

The new growth of cartilage (*c*) in front of the pointed lateral process of the hypobranchial plate is larger in size and has assumed a triangular shape. The thyrohyals are also larger and their posterior extremities are dilated. The thyroid foramen does not yet open, since the ceratobranchials, although separated from one another at their distal ends, remain connected proximally. These last remnants of the ceratobranchials are short and stunted, but, seeing how near to the completion of their metamorphosis larvæ with tail reduced to a mere knob must be, it is surprising that any branchial arches should be found at all. The first ceratobranchial is triangular in shape, but the other two are more rod-like. No trace of the fourth is now to be seen.

Stage 6. *Specimen measuring* 20 *mm. from snout to cloaca. Stump of tail* 1 *mm. Length of hind limb, extended,* 23 *mm. Length of fore limb, extended,* 11 *mm.* (Plate II. fig. 6.)

The ceratohyals are more slender than in the previous stage, and are of more uniform diameter throughout. They are thinnest where they bound the hyoglossal sinus laterally. The sinus itself is much wider than before, but not appreciably deeper. A couple of slight notches in its border still serve to show how far the ceratohyal cartilage is now situated from the median line. The ceratobranchials have entirely gone, and the thyroid foramen has opened out into a sinus. The thyrohyal (*t*) is thus formed by the persistence and enlargement of that part of the hypobranchial plate of the larva which forms the inner boundary of the thyroid foramen. It is a matter of great satisfaction to me to be able by the results of the present investigation to confirm the view which I first propounded in the case of *Pipa* (8. p. 106), and subsequently upheld in my paper on *Pelodytes* (9. p. 586).

Since the first ceratobranchial has in all the earlier stages been distinguishable from the hypobranchial plate, and has now disappeared, it is evident that it cannot form any part of the postero-lateral process of the adult hyoid as it does in *Pelodytes*. It cannot even be said that the pointed process of the hypobranchial cartilage to which it was attached becomes the aforementioned process, since this broadens out and fuses with the autogenous cartilage marked *c* in fig. 6, and only differentiates into antero-lateral and postero-lateral processes later.

Stage 7. *Completely metamorphosed specimen measuring* 20 *mm. from snout to cloaca. No trace of tail. Length of hind limb, extended,* 23 *mm. Length of fore limb, extended,* 11 *mm.* (Plate II. fig. 7.)

Although the specimens which form the basis of the descriptions of Stages 6 and 7 are hardly distinguishable by their external characters, it is evident from the hyobranchial skeleton that the one now under discussion is considerably the older. The cartilage is much bluer, and more transparent and hyaline, than in the preceding. The ossification of the thyrohyals is just beginning, a small differentiated tract being discernible in the middle part of

the rod. The ventral splint-bone has also begun to ossify. The ceratohyal is extremely slender and delicately curved; its thickest part lies just external to the body of the hyoid. The notches in the hyoglossal sinus have disappeared, so that it is now impossible to define the limits of the posteror copula and the ceratohyal cartilage. The pointed lateral process of the hypobranchial plate is no longer distinguishable as such, but has broadened out into a plate. The antero-lateral (*pal*) and postero-lateral (*ppl*) processes are already disposed as in the adult. Both are evidently secondary outgrowths, as Gaupp (3. p. 433 (4)) has already shown to be the case in *Rana*. The antero-lateral process is probably formed in great measure by the independent cartilages (*c*, fig. 6), which remained free until the present stage.

Stage 8. *Adult specimen measuring* 33 *mm. from snout to cloaca. Length of hind limb, extended,* 46 *mm. Length of fore limb, extended,* 20 *mm.* (Plate II. fig. 8.)

It is surprising how slight are the differences between the hyobranchial skeleton of the just metamorphosed animal and that of the fully-grown adult. The hyoglossal sinus has deepened considerably, so that it is now behind the antero-lateral sinuses, instead of being at the same transverse level with them as in Stage 7. The broadest part of the ceratohyal lies, as in Stage 7, just off the antero-lateral process. The ventral splint-bone is completely ossified, but the ossification does not extend into the subjacent cartilage. The bone is quite superficial, and can readily be dissected off. The thyrohyals are well ossified, the posterior extremities remaining cartilaginous and boot-shaped.

Summary.

In the hyobranchial skeleton of the early larva of *Alytes* there is an anterior copula which subsequently disappears and forms no part of the adult hyoid.

The posterior copula extends backward to the laryngeal sinus, and thus completely separates the two hypobranchial plates. It persists as the central part of the body of the hyoid.

The postero-lateral process of the adult hyoid cannot be identified with the base of the first ceratobranchial as it can in *Pelodytes*, but both the antero-lateral and postero-lateral processes are new formations, as in *Rana*.

The branchial bars or ceratobranchials of the larva form no part of the adult hyoid, but are entirely resorbed.

The thyrohyal is developed from that part of the hypobranchial cartilage of the larva which constitutes the inner boundary of the thyroid foramen.

List of Authorities referred to.

(A more complete bibliography on the Hyobranchial Skeleton of Anura will be found in papers 8 and 9 of the following list.)

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9. Ridewood, W. G.—"On the Structure and Development of the Hyobranchial Skeleton of the Parsley-Frog (*Pelodytes punctatus*)." Proc. Zool. Soc. Lond., 1897, pp. 577–595.
10. Stannius, H.—Handbuch der Zootomie, Th. ii. Buch 2. Zootomie der Amphibien. Berlin, 1856.

EXPLANATION OF PLATE II.

Fig. 1. Hyobranchial skeleton of *Alytes obstetricans*. Stage 1, p. 5. Dorsal view. (×4½.)
2. Same. Stage 2, p. 7. Dorsal view. (×4½.)
3. Same. Stage 3, p. 8. Dorsal view. (×5¼.)
4. Same. Stage 4, p. 8. Dorsal view. (×5½.)
5. Same. Stage 5, p. 9. Dorsal view. (×5½.)
6. Same. Stage 6, p. 10. Dorsal view. (×7½.)
7. Same. Stage 7, p. 10. Dorsal view. (×7½.)
8. Same. Stage 8, adult, p. 11. Ventral view. (×4.)

Reference Letters.

c. Autogenous cartilages in figs. 4–6.
ca. Anterior copula.
cb 1. First ceratobranchial.
cb 4. Fourth ceratobranchial.
ch. Ceratohyal.
cp. Posterior copula.
h. Hyoidean cornu.
hb. Hypobranchial plate.
hgs. Hyoglossal sinus.
ls. Laryngeal sinus.
pal. Processus antero-lateralis.
ppl. Processus postero-lateralis.
pr. Pars reuniens.
sp 3. Cartilaginous spiculum of the third branchial arch.
t. Thyrohyal.
tf. Thyroid foramen.
v. Ventral splint-bone.